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A New, Dimorphic Species of *Pyemotes* and a Key to Previously-Described Forms (Acarina: Tarsonemoidea)¹ ~1975-

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ABSTRACT

Two male and 2 female forms of a new, dimorphic species of *Pyemotes* from the scolytid *Phleosinus canadensis* Swaine are described and life history notes are presented. Only one type of female was found to be phoretic. Normal and phoretomorphic females can produce both normal and phoretomorphic daughters. Two species groups in *Pyemotes*, the *scolyti* group and the

ventricosus group, are recognized and comparisons of morphological and behavioral adaptations for phoresy are made. Crossing experiments involving several forms indicate the probable existence of several closely related species in the ventricosus group, these often overlapping in their choice of hosts. A key to males of the genus and to females of the scolyti group is presented.

Mites of the family Pyemotidae, and especially those of the genus Pyemotes, have been cited frequently in the literature since the first third of the 19th century. In most cases, these citations have been concerned with an instance or instances of (1) the mite's importance as a predator of various insects. (2) its medical importance to man, or (3) its unusual life history and/or structure. Since ca. 1885, most authors have assumed that they have dealt with a single species—the so-called "straw itch mite," P. ventricosus (Newport), and the literature concerned with this name is voluminous.

Krczal (1959a,b, 1963) described several new species of *Pycmotes*. He gave a good history of the genus (1959a), and suggested that *P. ventricosus* is really an uncommon species and may be restricted to Hymenoptera. He believed the species most commonly associated with stored products insects (therefore the common species of medical importance) to be *P. tritici* (La Grèze-Fossot and Montagné, 1851, *ncc* Targioni-Tozzetti, 1878), under which he synonymized 5 early names. Moser (1975) supports his view with biosystematic evidence.

Cross (1965) expressed doubt that a number of host-specific species of *Pyemotes* existed, as suggested by Oudemans (1936) and later by Krczal (1959a). His view was based upon the close morphological similarity of many species, host records at hand, and statements by various authors that members of widely divergent insect host taxa (usually laboratory cultures) were attacked simultaneously by the same species of *Pyemotes*. Moser et al. (1971) and Moser (1975) show, however, that genetic incompatibility great enough to result in hybrid sterility does exist among certain forms of *Pyemotes* and that several closely-related species seemingly occur. These species do exhibit broad and widely overlapping host ranges (Table 1).

Presently known species of *Pyemotes* fall easily into 2 groups, the *scolyti* group, containing *scolyti*, *parviscolyti*, and *dimorphus*, and the *ventricosus* group, containing the remainder of the species. Table 1 summarizes our knowledge of the geographical distribution and host relationships of these 2 groups, based

¹ Received for publication Sept. 25, 1974. ² Professor, Dept. of Biology, Univ. Alabama, Tuscaloosa 35486. ⁸ Res. Entomologist, Southern For. Exp. Stn., U.S. For. Serv., Pineville, LA 71360. only upon specimens identified by us or upon information recorded from type specimens. It is seen that most members of both groups are widespread in their geographic distributions. Many, if not most, are probably cosmopolitan, undoubtedly distributed unwittingly through commerce. Generally speaking, members of the ventricosus group have wide host ranges, but have been recorded (usually as ventricosus) most frequently from (1) stored grains or (2) laboratories or other establishments keeping insects in culture. However, natural infestations (i.e., infestations appearing apart from man-induced situations) are known to occur (Table 1).

Members of the *scolyti* group are more restricted in their host relationships, being associated only with various bark beetles.

The following key easily separates the males of most species. Females of the *scolyti* group may also be easily distinguished from one another, but we have not been able to separate satisfactorily the females of the *ventricosus* group. The forms designated by letters are undescribed.

Primary types of anobii, beckeri, parviscolyti, and schwerdtfegeri were examined, and topotypes of boylei were available, but we did not see types of herfsi, scolyti, tritici, ventricosus, and zwoelferi.

We conclude that *P. tritici* (LaGrèze-Fossot and Montagné, 1851), not *P. ventricosus* (Newport 1850), is the straw itch mite. *P. boylei* Krczal is considered to be a synonym of tritici (L.-F. & M.).

ARTIFICIAL KEY TO THE SPECIES OF Pycmotes

1(a).	Males 2
1(b).	Females
2(a).	All 4 pairs of prodorsal setae in a transverse line, or nearly so
2(b).	Placement of prodorsals variable, but at least one pair arising well behind the others 3
3(a).	Prodorsal setae arranged in 2 transverse rows of 2 pairs each, posterior 2 pair stout, similar to opisthosomatic setae pc1 and pc2 of 1st hysterosomal plateparviscolyti Cross & Moser
3(b).	Not as above 4
4(a).	First and 2nd hysterosomal terga distinct; all 4 setae of 1st tergum subequal, very short, the laterals arising near the posterior margin of the segmentscolyti (Oudemans)
4(b).	

Table 1.—Partial geographical and host distributions of the known species of the genus Pvemotes.^a

Name	:	Locality	Hostb
1.	entricosus group anobii Krczal, 1959a	El Modeno, Calif., U.S.A. Atlanta, Ga., and Rapides Parish, La., U.S.A. Atlanta, Ga., U.S.A. Northern Germany	Colony of Apis melifera (Apoidea) (F) (a) Phthorophloeus dentifrons (Scolytidae) (F) in Celtis occidentalis (b) Agrilis lecontei (Buprestidae) (F) in Celtis occidentalis (F) (a) Anobium punctatum (Anobiidae) (L) (b) Calandra granaria (Curculionidae) (L) Calandra oryzae (L) Anobium punctatum (L)
2.	beckeri Krczal, 1959a	Gulfport, Miss., U.S.A. Pineville, La., U.S.A. Arlington, Va., U.S.A. Germany	Lyctus planicollis (Lyctidae) (L) Scolytus multistriatus (Scolytidae) (L) "Wasp Nest" (F) (a) Anobium punctatum (L) (b) Calandra oryzae (L) (c) Calandra granaria (L)
3	. tritici (LaGrèze-Fossot & Montagné, 1851)	Hawaii, U.S.A. Cuba Sonora, Mexico Natchitoches, La., U.S.A. Savannah, Ga., U.S.A. Manhattan, Kansas, U.S.A.	 (a) Cryptotermes brevis (Kalotermitidae) (F?) (b) Araecerus levipennis (Curculionidae) (F) Lixophaga sp. (?) (a) Anthonomus grandis (Curculionidae) (L?) (b) "Ichneumonidae" (L?) "odynerine wasp" (Vespidae) (F) Oryzaephilus surinamensis (Cucujidae) (L) (a) Sitotroga cereallela (Curculionidae) (L) (b) Galleria mellonella (Galleriidae) (L)
4	. herfsi Oudemans	Germany Balatonakali, Hungary	 (a) Anobium punctatum (L) (b) Calandra granaria (L) (c) Calandra oryzae (L) Grapholitha molesta (Olethreutidae) (?)
5	schwerdtfegeri Krczal, 1959	Aylesbury, England Germany	Anobium punctatum (L) but cultured on S. multistriatus (L) Buprestidae
6	o. ventricosus	England	(a) Anthophora retusa (Apoidea) (poss. L)(b) Monodontomerus sp. (Chalcidoidea) (?)
7	. zwoelferi	Czechoslovakia Prague, Czechoslovakia So. France College Park, Md., U.S.A.	"Hymenopterous larvae in rose galls" (?) Galleria mellonella (L) Coleophora (Coleophoridae) (L?) Mayetiola rigidae in willow gall (Cecidomyiidae) (F)
8	3. n. sp. "A"	Daly City, Calif., U.S.A.	"Khapra beetle trap" (F?)
ç). n. sp. "B"	Gorogorszag, Hungary	"Tenebrionidae" (?)
10). n. sp. "C"	Augusta, Miss., U.S.A.	Contarinia sp. (Cecidomyiidae) leaf sheath of Pinus taeda (F)
	scolyti group l. scolyti (Oudemans)	Cedar City, Utah, U.S.A. Delaware, Ohio, U.S.A. Moscow, Idaho, U.S.A. San Bernadino, Calif. Holland, Germany, France N. Rawalpindi, Pakistan	Scolytus ventralis (Scolytidae) (F)° Scolytus multistriatus (L)° Scolytus multistriatus (F)° Scolytus multistriatus (?)° S. multistriatus & S. scolytus (?) "Bark beetles" in P. excelsa (?)
2	2. parviscolyti Cross & Moser	Allen Parish, La., U.S.A. Tegucigalpa, Honduras Cerro Potosi, N.L., Mexico	Pityophthorus bisulcatus (Scolytidae) (F)° "Boring dust", Pinus oocarpa (F) Scolytus sp. in Abies (?religiosa) (F)°
3	3. dimorphus n. sp.	New Hampshire, U.S.A.	Phleosinus canadensis (Scolytidae) in Thuja occidentalis (F)°

^a Only data obtained from specimens determined by Cross and from type specimens are listed here.

^b Letters in parentheses following names indicate that the source of the specimens was (L) laboratory culture, (F) field collection, or (?) unknown.

^c Phoretic on adult beetle.

5(a).	Opisthosomatic setae pc2 large, similar to opis-	6(a).	Setae pc1 long, similar to setae pe1; claw I
` ,	thosomatics pd_1 or pe_1 in size		larger; claw IV tooth-like, pointed apically;
5(b).	Setae pc2 smaller, not much longer and some-		external tibial solenidium short, not reaching
` ,	times shorter than setae pc_1 , and much smaller		base of claw 7
	than setae hd. or he.	6(b).	Setae bc_1 short, less than $\frac{1}{2}$ the size of setae

- pd₁; claw I smaller; claw IV elongate, tusklike, rounded apically; external tibial solenidium very long, reaching nearly to the tip of the elongated clawbeckeri Krczal
- 7(a). Third prodorsal seta shorter, not extending more than ½ its length beyond areolus of 4th prodorsal setaschwerdtfegeri Krczal
- 8(a). Seta c of trochanter IV short and slender, rarely reaching to tip of tarsus IV, less than ½ as long as pd_1 or $pc_1 \dots anobii$ Krczal
- 9(a). Setae pc_1 and pc_2 subequal in length and thickness, or pc_2 but slightly larger than $pc_1 cdots 10$

- 11(a). With the following combination of characters:

 3rd prodorsal seta short, usually only a little longer than the 2nd prodorsal and barely reaching the areolus of the 4th prodorsal; internal ventrals I nearly twice as long as external ventrals Iherfsi (Oudemans)
- 11(b). Third prodorsal longer, usually at least twice as long as 2nd prodorsal and reaching areolus of 4th prodorsal easily; internal and external ventrals subequal in length ... swoelferi Krczal

- 13(b). Posterior margin of prodorsum rounded, that of 1st hysterosomal tergum variable in shape ...15

- 15(b). Internal ventrals II arising well behind apodemes II, usually near center of ventrite; claw

- I and leg I usually not distinctly enlargedventricosus" group
- 16(b). Prodorsum and terga I-III without marked longitudinal, parallel striae ...dimorphus, n. sp.

Pyemotes dimorphus, n. sp.

This interesting species is the 3rd to be described in the scolyti group, and is morphologically and ethologically most similar to P. parviscolyti. Both sexes exhibit a marked dimorphism, its manner of expression differing between the sexes. "Normal" females are typically elongate, spindle-shaped, and less heavily sclerotized, whereas "phoretomorphic" females are shorter and much broader with greatly thickened legs and a markedly enlarged claw I (Fig. 4, 6, 7). Normal males have the same general facies as other males of Pyemotes of the scolyti group, while heteromorphic males are distinctly larger, possessing many greatly enlarged setae besides (Fig. 11, 14). A variable amount of duplication of certain pairs of setae often accompanies setal enlargement in heteromorphic males.

As in the other 2 members of the scolyti group, P. dimorphus appears to be restricted to small scolytid beetles. It was first found by Dr. Marcel Reeves, University of New Hampshire, attacking the cedar bark beetle Phleosinus canadensis Sw. in Northern Whitecedar, Thuja occidentalis L.

Terminology and measurements used here follow that of Cross (1965), except that (1) male body length is measured from internal ventral seta I to the poststernal seta, (2) female body length is measured as in Cross and Moser (1971), and (3) dorsal setae are named according to the system of van der Hammen (1970).

Diagnosis. Both forms of females separable from all others in the genus except scolyti and parviscolyti in that internal ventrals II arise immediately behind apodemes II. Separable from scolyti in that the hind margin of the prodorsum is rounded and without a median emargination. Differentiated from parviscolyti in lacking numerous longitudinal striae.

Both forms of males differ from those of all other *Pyemotes* in having 4 pairs of prodorsal setae arranged in a transverse row or nearly so. Further separable from *parviscolyti* in that the anterior setae of the 1st hysterosomal plate do not project beyond the posterior margin of the opisthosoma (normal male) or, if so, then more than one pair of posterior setae on the first first dorsal plate (heteromorphic male).

Description of Females.—"Normal" Female (non-gravid; Fig. 1-3, 5a, 8).—Length, 216 (216-247); width, 80 (72-82); body typically spindle-shaped;

^{&#}x27;Includes the following species: anobii, beckeri, herfsi, schwerdtfegeri, "nr. schwerdtfegeri", tritici (=boylei), ventricosus, zwoclferi, Sp.A, and Sp.B.

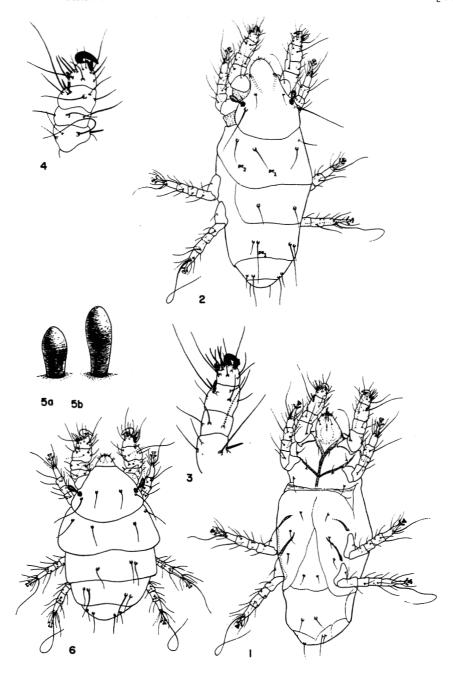


Fig. 1-9.—P. dimorphus, normal and phoretomorphic females.
Fig. 1-2.—Normal, ventral and dorsal aspects.
Fig. 3-4.—Right leg I, ventral. Fig. 3. normal; Fig. 4. phoretomorph.
Fig. 5a, b.—Solenidium of tarsus I, normal and phoretomorph, respectively.
Fig. 6.—Phoretomorph, dorsal aspect.

distinct longitudinal parallel striae lacking; all body setae thin, nude, flagellate.

Gnathosoma.—Comparatively narrow, width, 30 (28-32); palpal solenidium clavate, not extending beyond margin of gnathosoma.

Propodosoma. Dorsum.—Posterior margin rounded,

without median emargination; middle prodorsals fine, ½ (to ¾) length of anterior prodorsals.

Venter.-Angle between apodemes I acute; apodemes II distinctly oblique, making an angle of ca. 30° with anterior median apodeme, meeting (or approaching but not meeting) this apodeme; internal ventrals

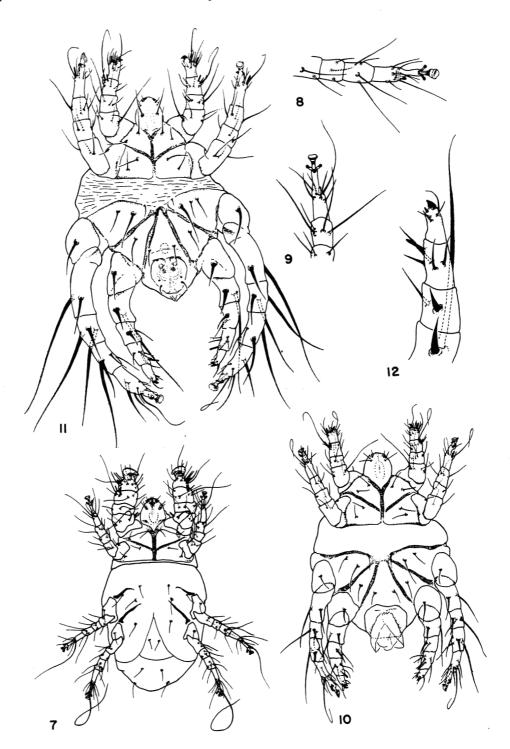


Fig. 7.—Phoretomorph, ventral aspect.
Fig. 8.—Normal, left leg II, ventral.
Fig. 9.—Phoretomorph, right leg II, ventral.
Fig. 10-19.—P. dimorphus, normal and heteromorphic males.
Fig. 10-11.—Ventral aspect. Fig. 10. normal; Fig. 11. heteromorph.
Fig. 12.—Heteromorph, right leg IV, ventral.

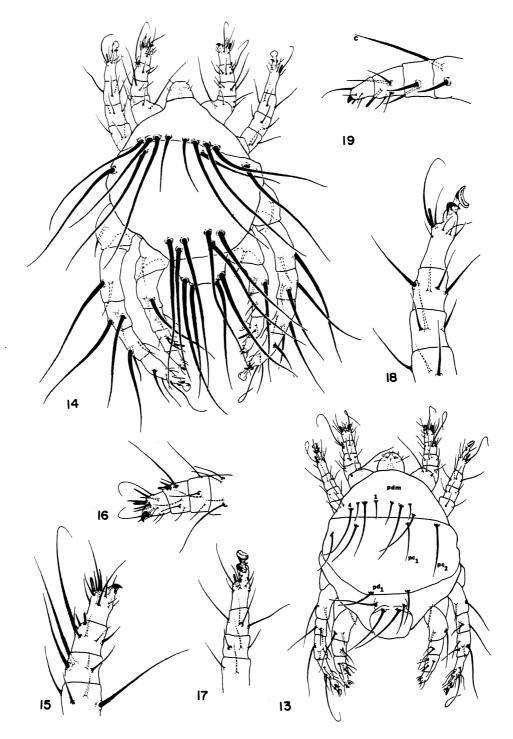


Fig. 13-14.—Dorsal aspect. Fig. 13. normal; pdm = prodorsum; 1 = first prodorsal; 4 = fourth prodorsal. Fig. 14, heteromorph.

Fig. 15.—Heteromorph, right leg I, ventral.

Fig. 16.—Normal, left leg I, ventral.

Fig. 17-18.—Right leg II. Fig. 17. normal; Fig. 18. heteromorph.

Fig. 19.—Normal, right leg IV, ventral.

II arising near apodemes II, their areolae nearly contiguous with the apodeme; internal ventrals II short, not reaching hind margin of plate.

Hysterosoma. Dorsum.—Posterior margin of 1st segment very broadly and shallowly emarginate, margins of remaining segments (except the last) slightly undulate; setae pc_1 distinctly posterior to pc_2 , short, not nearly reaching posterior margin of segment; setae pd_1 reaching slightly beyond segment II (or usually not); setae pe_1 longer than all other hysterosomal setae, shorter than (to subequal to) posterior prodorsal setae; setae of segment III arising in a transverse row (or, rarely, pe_1 arising behind pe_2); setae pf_1 arising slightly behind pf_2 ; setae pf_1 $\frac{3}{4}$ ($\frac{1}{2}$ — $\frac{3}{4}$) as long as pe_1 .

Venter.—Poststernal setae slightly closer together than opisthosomal sternals; opisthosomal ventrals only slightly larger than setae of segment V.

Legs.—Leg I, 18.4 (16.2–18.4) wide; leg II, 13.0 (11.9–13.0) wide; leg III, 70 (68–70) long; leg IV, 70 (70–73) long; length, ta IV, 24.8 (24.3–25.4); solenidium of ta I thickly clavate, arising at laterodistal angle of segment (Fig. 3, 5a); solenidium 1 (ti I) thinly strobilate, its areolus appearing contiguous with that of solenidium 2, but 2 arising well basad of 1 and reaching only ½ (to ½) of the distance to its tip; solenidium of ta II (Fig. 8) subapical, arising on a transverse line (or nearly so) between 2 flagellate setae; solenidia of ti II and ti III absent; tarsi II and III each with 6 tactiles.

Phoretomorphic Female (non-gravid; Fig. 4, 5b, 6-7, 9).—These females differ from the description of the "normal" females only in the characters cited here. Body comparatively shorter and broader than that of normal form.

Length, 197 (184–197); width, 100 (92–102); body, oval; dorsal body setae usually slightly longer and stouter than that of "normal" form.

Gnathosoma.—Width, 35 (27-36).

Propodosoma. Dorsum.—Anterior prodorsals comparatively long, reaching halfway (or nearly so) to posterior margin of sclerite.

Venter.—Internal ventrals II reaching posterior margin of plate (or beyond).

Hysterosoma. Dorsum.—Segments II (or II and III) with shallow, median emarginations (or margins linear); setae pd_1 reaching beyond (or as far as) hind margin of segment II; setae pe_1 shorter than posterior prodorsal setae; setae of third segment arising in a transverse line, or nearly so; setae pf_1 arising slightly behind pf_2 ; setae pf_1 34 as long as pe_1 .

Venter.—Setae of segment V stouter, slightly longer (or not) than opisthosomal sternals.

Legs.—Leg I and II wider than those of normal form. Leg I, 28.1 (21.1-29.7) wide; leg II, 15.1 (11.9-16.2) wide; leg III, 72 (63-74) long; leg IV, 75 (66-76) long; length, ta IV, 29.2 (24.3-30.2); solenidium of ta I resembling that of normal form but longer (Fig. 5b).

Description of Males.—"Normal" Male (Fig. 10, 13, 16-17, 19).—Length, 98 (95-105); all body setae flagellate apically, dorsals indistinctly spiculate, ven-

trals seemingly nude; body broadly elliptical in dorsoventral aspect.

Gnathosoma.—Dorsals small, nearly in a transverse line; palpal solenidium elongate and clavate, not extending more than ½ its length beyond anterior margin of gnathosoma.

Propodosoma. Dorsum.—Broad, hemispherical in dorsal aspect, hind margin linear; 4 pairs of setae (or 1 or more setae missing), the inner 3 pairs more or less in a transverse line, the outer (4th) pair posterior to these (or 1st and 3rd pairs anterior to 2nd and 4th); 1st and 3rd pairs of setae less than ½ the length of the 2nd and 4th, the latter 2 pairs elongate but not reaching areolae of posterior setae of dorsal plate.

Venter.—External ventrals I arising in front of apodemes II.

Hysterosoma. Dorsum.—First hysterosomal plate broad, rounded posteriorly (to rectangulate); all 3 pairs of setae of plate enlarged, similar to 2nd and 4th pairs of prodorsum; setae pc_1 arising slightly anterior to pc_2 (or both pairs in a transverse line); setae pd_1 distinctly closer together than pc_1 , their areolae touching hind margin of first dorsal plate (or nearly so); 2nd hysterosomal plate bearing 2 pairs of setae, the inner pair similar to setae pc_2 , the outer, anterior pair smaller, similar to pc_1 .

Venter.—Apodemes II-IV fused on each side; areolae of internal presternals arising on apodemes III, subequal to (usually shorter than) other setae of plate; external presternals the largest setae of plate, distinctly behind line drawn between 1st axillaries (or, rarely, these nearly in a transverse line); single pair of poststernals distinctly smaller than and arising well behind 2nd axillaries.

Legs.—Leg II, 68 (66–74) long; leg IV, 85 (85–110) long. Leg II, 16 (16–19) wide; leg IV, 18 (16–24) wide. Ta I distinctly longer than wide; claw I small, arising from a short pedicel at inner, apical margin of tarsus (Fig. 16); tarsi II and III obliquely truncate (or abruptly constricted) apically when viewed from the side; tarsi I and II each with a pronounced apical solenidium, that of tarsus II more rodlike than that of tarsus I; tr III distinctly arcuate; dorsal solenidium of ti IV in apical third of segment, subequal in length to the median (or median dorsal) seta; claw IV small but intact, its apex distinguishable; inner, most apical seta of tarsus IV enlarged bladelike or solenidionlike.

Description of Heteromorphic Male.—As described for the "normal" male except for the following: Length, 110 (110-130); all dorsal setae and most setae of legs and venter greatly increased in size (Fig. 11 and 14).

Gnathosoma.—Posterior ventrals extending more than ½ their lengths beyond gnathosomal margins; solenidium more elongate than in normal male, extending ca. ½ its length beyond gnathosomal margin.

Propodosoma. Dorsum.—Hemispherical to conical in dorsal aspect, hind margin linear; 4 pairs of setae in a transverse row, all greatly enlarged, the innermost (first) pair less than ½ the length of the other 3 pairs (or the 1st and 3rd pairs less than ½ as long

as the 2nd and 4th); 2nd-4th pairs reaching beyond areolae of setae of 2nd dorsal plate (or only 2nd and 4th pairs this long).

Venter.—Internal ventrals I and II distinctly longer than their respective external ventrals.

Hysterosoma. Dorsum.—First dorsal plate with 3 pairs of posterior setae (2-4 pairs), i.e., setae pd_1 duplicated at least once, their areolae not close to or contiguous with hind margin of 1st dorsal plate; 2nd hysterosomal plate bearing 2 (or 3) pairs of setae, the outer, anterior pair subequal to (or larger than) inner, posterior pair.

Legs.—Leg II, 106 (96-126) long; leg IV, 140 (126-156) long. Leg II, 22 (22-27) wide; leg IV, 22 (22-34) wide; no other characters differ from "normal."

Distribution.—Known only from New Hampshire, U.S.A.

Type Material.—Normal female holotype and normal male allotype from Tilton, N.H., May 1972, M. Reeves, from the galleries of Phleosinus canadensis in Thuja occidentalis. Six "normal" female paratypes (No. 1-6) with data as for types. Five phoretomorphic female paratypes (No. 9-13) with data as for types. One phoretomorphic female paratype (No. 14) Tilton, N.H., Sept. 30, 1968, J. Conklin, P. canadensis in T. occidentalis. Two phoretomorphic female paratypes (No. 7-8) from Haverhill, N.H., June 1972, M. Reeves, phoretic between coxae I and II of Phleosinus canadensis from Thuja occidentalis. Two normal male paratypes (No. 15-16) with same data as types. One normal male paratype (No. 17) Tilton, N.H., Sept. 30, 1968, R. H. Hutchins, same hosts. Five heteromorphic male paratypes (No. 18-22) with same data as types.

Type Repositories.—Holotype, allotype, and paratypes 1, 7, 8, 18 in the U.S. National Museum. Paratypes 2, 14, 17, 19 in the Snow Entomological Collections, The University of Kansas. Paratypes 3, 9, 15, 20 in the Zoological Museum, The University of Hamburg. Paratypes 5, 11, 22 in the British Museum (Natural History). Paratypes 4, 10, 21 in the Hungarian National Museum, and paratypes 6, 12, 13, 16 in the personal collection of the senior author.

Life History.—Bolts of beetle-infested *Thuja occidentalis* were sent to the junior author, who made the following observations in the laboratory.

Parasitization of *Phleosinus canadensis* by *Pyemotes dimorphus* was relatively infrequent, the estimated rate being 5-10%. Both forms of both sexes coexisted in the galleries of *P. canadensis*, and both types of female feed upon eggs, larvae, and pupae of the beetle. Daughters of those females attacking eggs often appeared to be trapped in the egg niche, being unable, like certain members of the tarsonemoid genus *Iponemus* (Lindquist 1969) to penetrate the plug. These young females literally poured from the niche when the plug was broken.

On the basis of a single observation (a normal female mated by a heteromorphic male), birth and mating behavior was essentially the same as described for *Pyemotes parviscolyti* (Moser et al. 1971). Fe-

males were born head first, aided by the male, after which copulation follows immediately. In *P. dimorphus*, birth took ca. 10 s, copulation ca. 6 s.

The ratio of phoretic mites on beetle brood vs. parent adults was the same as that for Pyemotes parviscolyti. About 70% of the brood adults (primary attackers), but only ca. 15% of the parent adults (those re-emerging and attacking for 2nd time) of P. canadensis carried female P. dimorphus. About 300 beetles were checked as they emerged from rearing cans containing infested limbs. As many as 4 females were found on a beetle, but most carried 2. They typically rode attached to coxae 1 and 2. If the beetle died, the mites remained attached and perished with it. We saw no evidence of mites attacking adult beetles.

Only heteromorphic females were phoretic. Since their first claw is much larger, their legs, particularly the first pair, are much stouter, and the body form is much more compact and sclerotized than in the normal form, it seems clear that, in this species, the heteromorph can be said to constitute a primitive phoretic stage. In a genus in which structural specializations for dispersal and adaptations for survival during the dispersal period are rare, the evolution of such a stage is of particular interest.

Several authors mention "nymphal" (Reuter 1900, 1909, Krczal 1959a, Rack 1972) or "2nd larval" (Gurney and Hussey 1967) stages in the life cycles of Siteroptes graminum and Pediculaster mesembrinae, respectively. Rack (1972) found that, in the case of S. graminum, all "nymphs" were sexually capable; indeed, their reproductive rate often exceeded that of the "females." It is our belief, at least in the case of S. graminum, that the "nymph" is simply an adult analogous to the "normal" form of P. dimorphus. These may give rise to heteromorphic adults more capable of dispersing—overwintering.⁵ Rack (1972) mentions that "adults" have thicker legs and more heavily sclerotized cuticle, these presumably analogous to the phoretomorphic form of P. dimorphus. She found "adult," i.e., heteromorphic forms, only in late summer. As she suggests, direct environmental stimuli (food, climatic factors, etc.) probably govern the timing and direction of this polymorphism.

The appearance of polymorphic dispersal-overwintering forms, therefore, seems to have occurred independently in at least 2 closely related genera of Pyemotidae. We suspect that more than the 2 or 3 species cited above are involved. It is also quite possible that more than 2 polymorphic forms may exist in some species.

Table 2 contrasts characteristics of the 2 species groups of *Pyemotes* with respect to adaptations for dispersal. Members of the *scolyti* group are variously adapted for dispersal by phoresy while all members of the *ventricosus* group appear not to be. Herfs (1926), Krczal (1959a), and others have reported that newborn, mated females, at least of *herfsi* and *scolyti*, must find a host within 48 h after they leave the mother or they will die, presumably of starvation.

⁵ Rack (personal communication) has independently reached the same conclusion and will so state in a paper still in press.

Table 2.—Comparison of the 2 species groups of Pyemotes for specialized characteristics presumed to be adaptive for dispersal.

Characteristics	P. scolyti group	P. ventricosus group				
Physical characteristics						
1. Shortened, compact body shape	P. scolyti and heteromorphic dimorphus only	None				
2. Thickened legs I	Yes	No				
3. Enlarged claw I	Yes (except for normal dimorphus)	No				
4. Females phoretic	Yes	Not as far as known				
5. Ability to survive during dispersal	Greater*	Lesser?				
6. Form specialized for phoresy	Yes (in dimorphus)	No				
Behavioral characteristics						
1. Mites attack adult hosts	No	Yesb				
2. Host range	Narrower	Broader				

Moser et al. (1971) found, however, that survival of young female parviscolyti in the laboratory is at least partly dependent upon humidity. Unfed females held at 100% relative humidity survived more than 5 times as long (ca. 7 days) as females held at lab humidities of ca. 40% (ca. 1.4 days). Presumably, these former females could survive long enough to find a phoretic host with a high probability and also survive flights of some distance, particularly at night.

No species of the scolyti group is known to attack an adult host, while at least some species of the ventricosus group do so regularly. Krczal (1959a) suggested that phoretic adult female scolyti were able to remain alive by feeding from the beetles upon which they rode. Presumably, the beetle is not harmed by the feeding. He suggested this feeding to be a specialization for dispersal. It seems unlikely that feeding can occur from the beetle unless it is punctured, and it seems equally unlikely that puncturing could be accomplished without envenomization. However, the matter remains only speculation. We agree with Krczal's observation that the wide host range of members of the ventricosus group is a means of survival for an animal whose dispersal abilities are limited.

P. dimorphus reluctantly attacked brood of its natural host, P. canadensis, in the laboratory. Unlike all other Pyemotes tested, we could not induce females to feed on 2 other scolytid larvae, Dendroctonus frontalis Zimmerman and Scolytus multistriatus (Marsham). Like the other members of the scolyti group, it was relatively "venomless," the host remaining alive for about a day after the initial attack.

Three females became physogastric in the laboratory and the types of their offspring were ascertained (Table 3). Two of the 3 died prior to producing an (assumed) normal number of offspring, but all 3 were less fecund than females of other species investigated by us. Birth of progeny for all 3 females began ca. 7 days after mating. Mother no. 1 continued to give birth for 12 days after the 1st male was born.

Table 3.—Numbers and kinds of progeny born to 3 laboratory-reared P. dimorphus females.

			Subsequently born progeny				Unborn progeny ^d				
Mother ^{a, b}		First-born progeny		Females		Males		Females		Males	
		First-		Nor- Hetero-	Hetero-	Nor- Hete	Hetero-	Nor-	Hetero-	Nor-	Hetero-
No.	Type	born	Type	mal	morphic	mal	morphic	mal	morphic	mal	morphic
1	Normal	18	Long hair	12	9	0	0		1	0	0
2°	Fat	18	Short hair	0	6	0	0		7	0	0
3°	Normal	18	Long hair	0	8	0	1		34	0	0

See text.
 See Krczal 1958a, Moser (in press).

Father unknown.
 All 3 mothers reared on pupae of Phloeosinus canadensis.
 Mother died prematurely 12 days after giving birth to 1st male.
 Dissected from mother after her death.

Unlike other species of *Pyemotes* studied by us, maturation of embryonic *P. dimorphus* may occur nearly simultaneously, a characteristic previously noted in *Elattoma bennetti* (Cross and Moser 1971).

Although the clearcut dimorphism of both sexes indicates a simple chromosomal aberration (e.g., a deletion) or single point mutation, no simple mode of inheritance appears to be typified by our present data (Table 3), particularly if the assumption of arrhenotoky is made. Reduced viability or lethality of the mutant may be indicated by the reduced number of offspring.

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ERRATA

Table 3. "Long-hair" males refer to heteromorphic males. "Short-hair" males refer to normal males.

A fuller explanation of the phoretomorph concept appears in the "Annals", 68(5).